BIOGEOGRAPHY AND MANAGEMENT OF NATIVE WESTERN SHRUBS: A CASE STUDY, SECTION TRIDENTATAE OF *ARTEMISIA*

E. Durant McArthur and A. Perry Plummer[1]

Abstract.—Biogeographical considerations are important in the management of western shrublands. Seedings on rangelands have a higher probability of success when tried and tested principles are followed. It is usually best to seed mixtures that include adapted shrubs and herbs. Shrubs generally are well adapted to the environmental extremes of western ranges. Throughout the year, they provide nutrients for herbivores that are only sea sonably available in herbs.

Section Tridentatae of *Artemisia* is endemic to western North America and distinct from the analogous Eurasian section (or subgenus) Seriphidium. The groups have separate, distinguishable centers of diversity; the two groups seem to be connected in the geologic past by way of the more primitive subgenus Artemisia. Preliminary karyotypic evidence suggests different but advanced karyotypes for both groups; chemotaxonomic and morphological data indicate differences in the groups. The Tridentatae likely evolved in North America during late Tertiary or early Quaternary times under the stimulus of cycles of aridity.

The Tridentatae (sagebrushes) are morphologically variable. Different accessions are differentially adapted. Management practices for various taxa should take into consideration the individual taxon's characteristics. Effort should be made to seed adapted taxa and accessions. Sagebrush management requires maintenance, seeding, or thinning, depending upon the circumstances.

Aside from serving as a review of the lit erature, this paper presents original data and touches upon unpublished material and reports being prepared for publication.

Shrubs are an important component of the vegetation of the American West, as well as in other parts of the world. In fact, much of the West is classified as shrubland because the dominant plant species are shrubs (Küchler 1964, McGinnies 1972). Plummer (1974) recognized six major shrub land types in the American West.

Since the arrival of the white man, shrub ecosystems have been exploited and despoiled by his livestock and land management practices (Cottan 1961, Heady 1975). The distribution and composition of many plant and animal communities have been substantially altered. The relatively new sci ence of range management was born, in part, to systematize efforts to make shrublands more productive. The value of shrubs in their own right has long been under-

estimated (McKell 1975b). In fact, much ef fort, time, and money have been spent to eradicate and control shrubs in order to fa cilitate the establishment of exotic grass monocultures.

Shrubs have many current and potential uses. In the proceedings of an international symposium on useful wildland shrubs (McKell et al. 1972), a section on the present and possible uses of shrubs included chapters devoted to browse and cover for wildlife, low-maintenance landscaping, soil cover and stabilization, fire relations, medicinal values, and industrial raw materials. This list was not exhaustive; for example, no reference is made to the use of shrubs as food for livestock.

Our work on shrubs began with a need to improve critical winter game ranges (Plummer et al. 1968) and has continued with emphasis shifting to improving all types of disturbed sites (McArthur et al. 1974, Monsen 1975, Plummer, in press). Numerous

[1]Research geneticist and project leader, Intermountain Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture, Ogden, Utah 84401; located at the Intermountain Station's Shrub Sciences Laboratory, Provo, Utah 84601.

species and ecotype adaptation plots have been set out both in and out of the natural ranges of particular shrub taxa. Plummer (in press) listed 85 native and 14 exotic shrubs that have proved to be adapted to disturbed sites in one or more vegetative communities of the Intermountain Region. Some shrubs can be established only vegetatively or by transplanting and do not reproduce by seed. Even these, however, have value since they cover and stabilize disturbed areas and serve as a nurse crop on critical sites for plants that establish more slowly.

A principal thrust of range management has been in the modification of vegetation— often disclimax vegetation (Heady 1975). Mechanical, chemical, and burning methods have been used widely to control unwanted plants—mostly woody ones—on rangelands. These treatments are generally followed by seeding. Practical trials and experiments have succeeded and failed often enough for cause and effect relationships to be ana- lyzed and to serve as a set of principles. Recommendations relative to the seeding of many range sites can be made with a high probability of success. Plummer et al. (1968) and Heady (1975) outlined procedures and site criteria necessary for successful range seedings. Except for weather conditions, these are controllable by the range man- ager. We wish to emphasize, as did Plum- mer et al. (1968) and Heady (1975), the im- portance of planting mixtures of adapted taxa because:

(1) Many seedings are on variable terrain that includes diverse microhabitats.

(2) A mixed diet is usually more palatable to and nutritious for herbivores.

(3) Periods of growth vary for different plant taxa and classes (shrubs, forbs and grasses); so succulent forage is provided for a longer time.

(4) Some plants benefit others by provid- ing habitat and nutrients.

(5) Diseases and insect pests do not at- tack all species equally. Shrubs should be included in most seedings since they are well adapted to drought, salinity, acidity, wide temperature fluctuations, and other environmental extremes of western ranges. In addition, they provide habitat for ani-

mals that other classes of plants do not (McKell 1975a).

This paper examines the biogeography and the management implications of a par- ticular group of shrubs—the sagebrushes, section Tridentatae of *Artemisia*. The sage- brushes are perhaps the most common shrub in western North America. In order to get a better idea of how to better manage and utilize this resource, we have tried to catch a glimmer of its evolutionary past. Such in- formation should benefit the management of sagebrush ranges by providing bases for bet- ter understanding species adaptation and distribution and plant improvement pro- grams through hybridization and selection.

Methods and Materials

Species Distributions.— General distribu- tion of species of the Tridentatae was ob- tained from Ward (1953), Beetle (1960), and by examining the *Artemisia* collections of the herbaria of Brigham Young University (BRY) and the Intermountain Station's Shrub Sciences Laboratory (SSLP). We have followed Beetle's (1960) and Beetle and Young's (1965) nomenclature for the Triden- tatae (Fig. 1). Distribution of the Seriphi- dium species that occurs in the Soviet Union was taken from Polyakov (1961). For spe- cies that occur outside the Soviet Union, de Candolle (1838) and Boissier (1875) were consulted (Fig. 2). We reviewed other re- gional and national floras peripheral to the Soviet Union but found little information to add to the aforementioned references.

Karyotyping.— The karyotypes of section Tridentatae were obtained from a prelimi- nary analysis of data for a later report (McArthur, Pope, and Plummer, in prepara- tion). A sample cell was selected from each of 13 diploid and 14 tetraploid populations representing 9 diploid and 9 tetraploid taxa. Squashed root tips of seedlings were micro- scopically analyzed. The slides were pre- pared by fixing colchicine-pretreated root tips in 1:3 acetic alcohol and squashing them in acetocarmine. The idiogram of sec- tion Tridentatae (Fig. 3) was prepared from measurements made on 20 X 25 cm photo- micrographic prints at a magnification of 3120X. The idiogram for the two species of
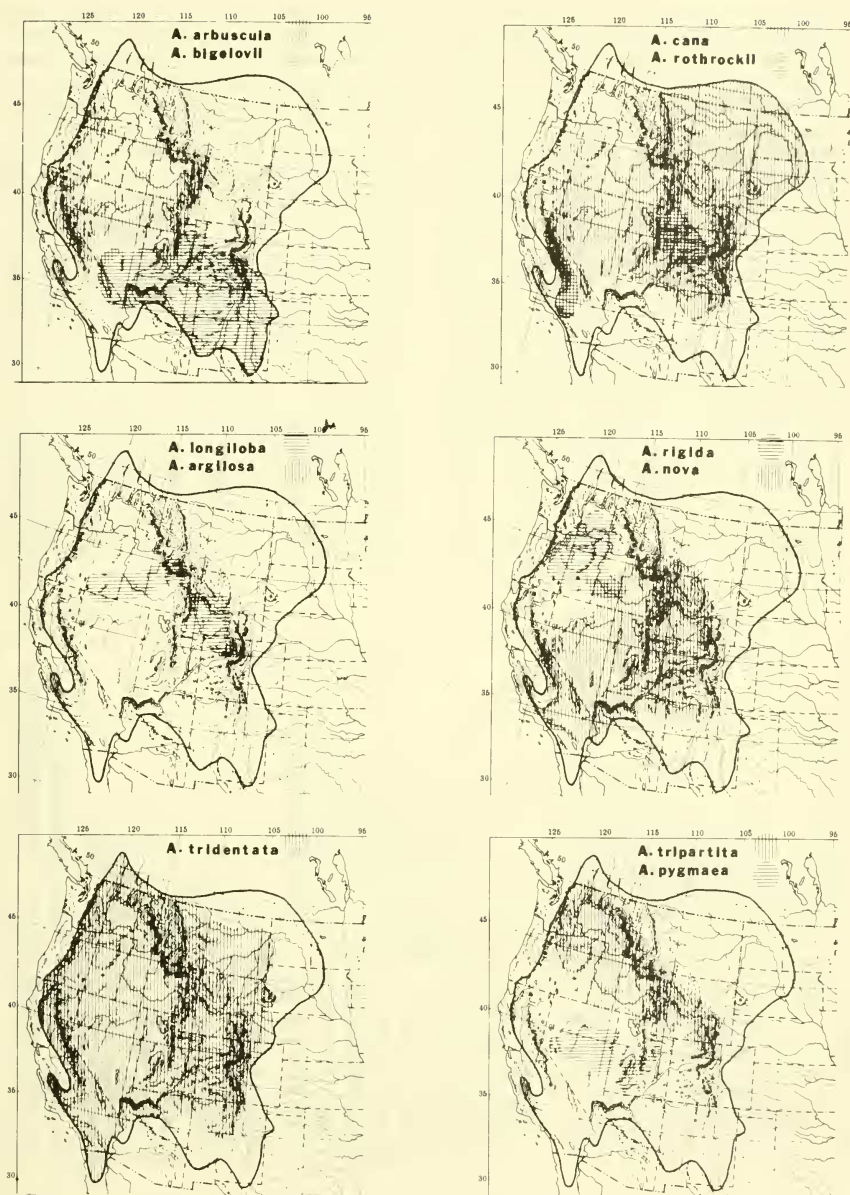
Fig. 1. Distribution ranges of the species of section Tridentatae.

Seriphidium (Fig. 3) was prepared from data presented by Filatova (1974). We used the shorter of two lengths Filatova gives for chromosome 3 of *A. juncea*. Chromosome sizes (L = large, M = medium, S = small) were determined by pairing the chromosomes according to relative length and centromere position, dividing the genome into relative lengths, averaging the length of each pair, and proportionalizing the pair so the genome had a length of 100 arbitrary units. Thus, L > 12.4, M = 9.6 — 12.4, S < 9.6 for diploids and L > 6.2, M = 4.8 — 6.2, S < 4.8 for tetraploids. The centromere positions (M = metacentric, SM = submetacentric, and ST = subterminal) were determined by the ratio of the length of the short arm to the length of the long arm. Thus, M > 75 percent, SM = 50 — 75 percent, ST < 50 percent (Tables 1 and 2).

Species Adaptation.— Shrub wildings have been collected in the spring (March-June) and fall (October-November) and transplanted to uniform gardens and smaller species adaptation plots. Periodic ratings are made as to their height, crown, vigor, herbage yield, reproduction, and survival. These data are on file principally at the Great Basin Experimental Area in Ephraim, Utah, but also at the Shrub Sciences Laboratory in Provo, Utah. Collection numbers, prefixed by a U, have been assigned to accessions within each taxon (Tables 1, 2, 3). Voucher herbarium specimens are deposited at the Shrub Sciences Laboratory (SSLP).

Section Tridentatae of Artemisia

The genus *Artemisia* is a group of about 200 plant species which belong to the tribe Anthemideae of Compositae (de Candolle 1837, Clapham 1962). Good (1974) considers *Artemisia* as belonging to his temperate genera, group 1, subgroup 2, which includes
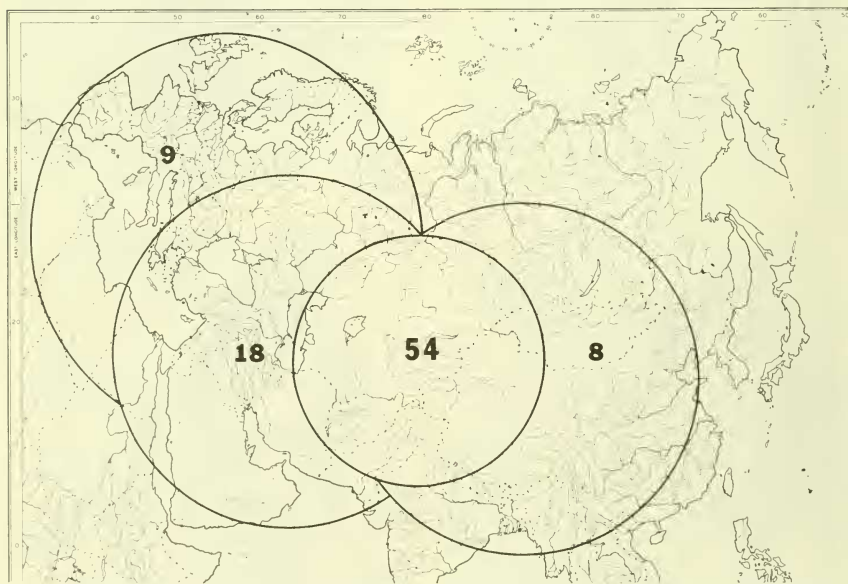

Fig. 2. Distribution of the section (subgenus) Seriphidium in Eurasia and North Africa. The numbers indicate maximum number of species in each area.

"genera found throughout the northern ex-tratropical latitudes with some extension southwards in all directions, usually to cer-tain tropical mountains only."

Besser (1829) began the first com-prehensive monograph on the genus early in the 19th century. He recognized four sec-tions—Abrotanum, Absinthium, Dracunculus, and Seriphidium. His monograph was not completed before he died, but de Candolle's (1837) "Prodomus Systematis Naturalis" and Hooker's (1840) "Flora Boreali-Americana" include significant portions of Besser's work. Besser's sections are still considered the principal divisions of the genus, but in some treatments they have been elevated to the rank of subgenus and additional subordinate sections created (Rydberg 1916, Polyakov 1961). The comprehensive treatment of *Ar-temisia* in the "Flora of the USSR." (Poly-akov 1961) unites Absinthium and Abrota-num into the single large subgenus Artemisia. Hall and Clements (1923) recog-nized the close affinity of these two groups, which were separated in Besser's scheme

only by the hairiness of the floral recep-tacle. Members of Seriphidium are distin-guished by having only perfect disk flowers whereas members of the other subgenera have fertile or sterile ray flowers and vari-ous degrees of disk flower fertility. Rydberg (1916), while recognizing the subgenus Seri-phidium, created the section Tridentatae for most North American members of Seriphi-dium. He also created monotypic sections for *A. rigida* and *A. pygmaea* as well as a new genus for the largely herbaceous *A. palmeri*. More recent monographers (Hall and Clements 1923, Ward 1953, and Beetle 1960) have been more conservative than Rydberg, but have been divided on the re-tention of Tridentatae as a section. Beetle (1960) included all woody, North American, homogamous *Artemisia* species in the sec-tion Tridentatae along with *A. bigelovii*, which often has a ray flower or two on oth-erwise discoid heads. Beetle's Tridentatae form a group of 11 unequal species endemic to western North America (Fig. 1). The spe-cies distribution ranges vary in size from
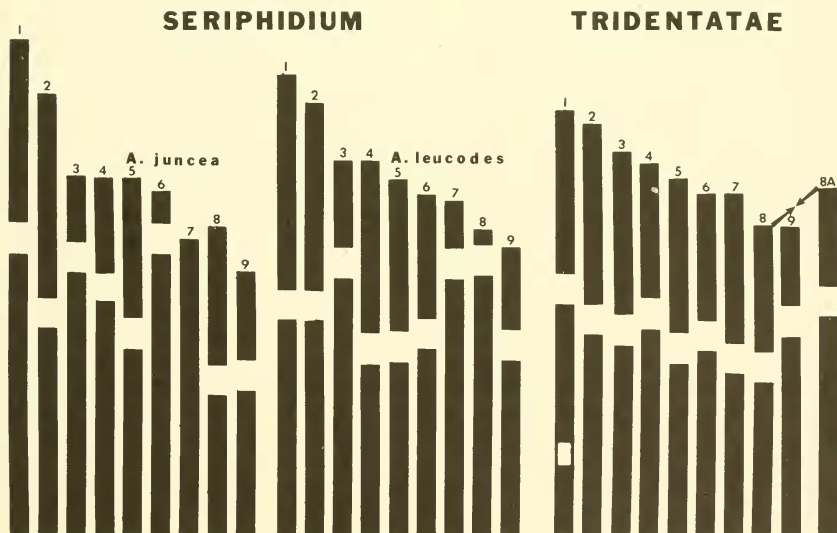

Fig. 3. Idiograms of two species of section Seriphidium, *A. juncea,* and *A. leucodes* (after Filatova 1974) and a generalized idiogram of section Tridentatae. Note secondary constriction in long arm of the first chromosome in the Tridentatae. The arrows indicate a chromosome substitution in some taxa (Table 1).

TABLE 1. Chromosome constitution of representative diploid Tridentatae.

Taxon	Collection data	1		2		3		4		5		6		7		8		8A		9	
		trl[a]	rll[b]	trl	rll	trl	rll	trl	rll	trl	rll	trl	rll	trl	rll	trl	rll	trl	rll	trl	rll
Artemisia arbuscula	U1-Paradise Valley, Humboldt Co., Nevada	12.5	7.2	12.5	6.5	11.8	6.3	11.6	6.7	10.6	5.8	10.6	6.2	10.8	5.6			10.6	7.2	10.1	7.2
A. arbuscula	U4-Widtsoe, Garfield Co., Utah	11.9	7.1	11.9	6.2	11.7	6.2	11.9	7.1	11.4	5.9	11.0	6.9	10.0	5.3			11.0	7.9	9.5	6.8
A. bigelovii	U9-Flagstaff, Coconino Co., Arizona	13.8	8.4	13.0	6.7	12.1	6.3	11.7	6.7	11.7	6.3	10.7	6.1	11.7	5.9			10.7	7.5	9.2	6.4
A. cana	U10-Nolan Station, Carbon Co., Utah	13.2	7.3	13.0	6.5	12.1	6.4	11.7	4.0	10.3	5.2	9.5	5.6	10.3	5.7	9.3	4.7			9.3	6.0
A. nora	U13-Huntington, Emery Co., Utah	13.0	8.0	13.0	7.3	11.9	6.5	11.6	8.2	11.1	5.7	10.8	6.0	10.8	5.7	8.7	5.4			8.9	6.5
A. rigida	U3-LaGrande, Union Co., Oregon	13.8	8.1	12.6	6.7	11.4	6.3	11.8	6.9	9.8	4.9	10.3	6.1	10.2	5.6			10.1	6.8	9.1	6.4
A. rothrockii	U1-Swasey Ridge, Sanpete Co., Utah	14.3	8.1	13.0	6.7	11.3	6.7	12.1	7.4	10.0	5.4	10.8	6.5	9.7	5.0	10.0	5.3			8.7	7.4
A. tridentata tridentata	U44-Loa, Wayne Co., Utah	12.6	7.6	12.6	6.9	11.8	6.3	10.1	6.6	11.1	6.0	9.8	6.5	9.8	5.1	8.8	5.2			8.9	6.7
A. tridentata tridentata	U63-Franklin, Franklin Co., Idaho	14.2	8.4	12.5	6.4	12.2	6.3	11.7	7.1	11.7	6.1	9.6	5.8	10.2	5.3	8.6	4.8			7.6	5.1
A. tridentata vaseyana	U9-Benmore, Tooele Co., Utah	12.6	7.1	13.2	7.0	13.0	7.3	11.6	6.6	11.2	6.0	11.6	7.2	10.0	5.2	9.3	5.2			9.3	6.4
A. tridentata vaseyana	U28-Dowd Springs, Daggett Co., Utah	13.3	7.7	12.7	7.1	11.4	6.1	10.5	6.3	11.0	5.7	10.5	6.3	10.1	5.4	10.1	5.8			9.7	6.7
A. tridentata tridentata	U36-Boise, Ada Co., Idaho	13.6	7.4	13.4	6.8	11.8	6.5	10.5	6.5	11.0	5.8	10.0	5.8	10.5	5.5	9.4	5.2			9.4	6.3
A. tripartita	U2-Dubois, Clark Co., Idaho	12.4	7.4	12.5	6.8	11.6	6.1	11.6	6.8	10.9	5.7	9.7	6.3	10.9	5.5	9.1	4.6			10.3	7.1
x̄		13.2	7.7	12.8	6.7	11.8	6.4	11.4	6.9	10.9	5.7	10.4	6.2	10.4	6.2	9.3	5.1	10.6	7.4	9.2	6.6
sc		.2	.1	.1	.1	.1	.1	.2	.1	.2	.1	.2	.1	.2	.1	.2	.1	.2	.2	.2	.2
Type[c]		LSM		LM		MM		MSM		MM		MSM		MM		SM		MST		SST	

[a] trl = total relative length of chromosome
[b] rll = relative length of long arm of chromosome
[c] Chromosome types: the first letter stands for chromosome size. L = large, M = medium, S = small. The other letters stand for centromere position. M = metacentric, SM = submetacentric, ST = subterminal. Some of the LSM have an obvious secondary constriction (Fig. 3); others do not.

those that cover most of the range of section Tridentatae (*A. tridentata* and *A. cana*) to relatively small ranges covering about 10 percent of the section's range (*A. pygmaea* and *A. longiloba*) to the restricted type location range of *A. argilosa*. *A. rothrockii* is shown with a disjunct range (Fig. 1). Ward (1953) and Cronquist (1974) maintain that *A. rothrockii* is restricted to the Sierra Nevada and its outliers. Beetle (1960), on the other hand, records the species from the Rocky Mountains. The California material is tetraploid and hexaploid (Ward 1953), whereas our work indicates that Rocky

Mountain material (from Utah's Wasatch Plateau) is diploid (McArthur, Pope, and Plummer, in preparation). The Rocky Mountain material may be an undescribed taxon. However, in this paper, we are treating it as *A. rothrockii*.

EVIDENCE FOR SEPARATING TRIDENTATAE FROM SERIPHIDIUM

Regardless of the rank (subgenus or section) that one attaches to Tridentatae or Seriphidium, the two taxa should be separated. Hall and Clements (1923), Ward

TABLE 2. Chromosome constitution of representative tetraploid *Tridentatae*.

Taxon	Collection data	Chromosome pair types[a]							
		LSM	LM	MM	MSM	MST	SM	SSM	SST
Artemisia arbuscula	U3-Antimony, Garfield Co., Utah	3	4	2	3	1	1	2	2
A. bigelovii	U9-Flagstaff, Coconino Co., Arizona	2	2	5	3	1	2	1	2
A. bigelovii	U13-Chinle, Apache Co., Arizona	3	2	5	3	1	2		2
A. cana	U3-Strawberry Reservoir, Wasatch Co., Utah	2	4	4	2	1	1	2	2
A. nova	U16-John's Valley, Garfield Co., Utah	3	1	6	2	1		3	2
A. nova	U22-Steinaker Reservoir, Uintah Co., Utah	3	1	5	3	2	2	1	1
A. pygmaea	U1-John's Valley, Garfield Co., Utah	2	2	6	4	1		1	2
A. rigida	U5-Elder Flat, Monow Co., Oregon	2	1	8	3	2			2
A. tridentata tridentata	U75-Wingate Mesa, San Juan Co., Utah	2	4	4	2		2	2	2
A. tridentata tridentata	U89-Steptoe Valley, White Pine Co., Nevada	2	4	4	2		2	2	2
A. tridentata vaseyana	U14-Colton, Utah Co., Utah	2	2	6	3		2	1	2
A. tridentata vaseyana	U23-Pinto Canyon, Washington Co., Utah	2	2	6	3	2		1	2
A. tridentata wyomingensis	U61-Milford, Beaver Co., Utah	2	2	8	3		1	1	1
A. tridentata wyomingensis	U80-Jacob's Lake, Coconino Co., Arizona	2	3	6	3		2		2
Average		2.3	2.4	5.4	2.8	.9	1.2	1.2	1.8
Expected		2.0	2.0	6.0	4.0	0	2.0	0	2.0

[a]Chromosome types: The first letter stands for chromosome size; L = large, M = medium, S = small. The other letters stand for centromere position; M = metacentric, SM = submetacentric, ST = subterminal. Some of the LSM have an obvious secondary constriction, others do not.

TABLE 3. Establishment and survival of *Artemisia tridentata* wilding transplants at the Snow Field Station, Ephraim, Utah.

| Subspecies | Collection data | Number of plants | | | Percent 1976/1971 | Vigor[a] | Repro-duction[b] |
		Initial (1969-1970)	Established (1971)	Survivors (1976)			
Tridentata	U44-Loa, Wayne Co., Utah	33	17	11	64.7	4	7
	U74-Dove Creek, Dolores Co., Colorado	40	31	25	80.6	9	10
	U75-Wingate Mesa, San Juan Co., Utah	47	36	22	61.1	7	4
	U76-Clear Creek Canyon, Sevier Co., Utah	44	33	21	63.6	6	5
	U79-Dog Valley, Juab Co., Utah	46	46	44	95.7	10	10
	U82-Brush Creek, Uintah Co., Utah	25	21	14	66.7	7	7
Total		235	184	137			
Mean					74.4	6.1	7.2
Vaseyana	U13-Indian Peaks Beaver Co., Utah	41	41	24	58.6	6	7
	U14-Colton, Utah Co., Utah	74	65	45	69.2	8	3
	U15-Sardine Canyon, Cache Co., Utah	41	24	20	83.3	5	7
	U19-Salina Canyon, Sevier Co., Utah	17	9	7	77.8	3	4
	U23-Pinto Canyon, Washington Co., Utah	36	28	26	92.9	7	7
	U24-Clear Creek Canyon, Sevier Co., Utah	44	34	12	35.3	4	3
	U31-Durkee Springs, Sevier Co., Utah	32	28	14	50.0	7	2
	U52-Alton, Kane Co., Utah	16	7	3	42.9	3	6
	U72-Petty Bishop's Log, Sanpete Co., Utah	124	99	88	88.9	8	8
Total		425	335	239			
Mean					71.3	5.7	5.2
Wyomingensis	U17-Milford, Beaver Co., Utah	41	15	10	66.7	7	4
	U37-Evanston, 23 Uinta Co., Wyoming	23	8	4	50.0	8	2
	U58-Trough Springs, Humboldt Co., Nevada	63	26	14	53.8	5	3
	U80-Jacob's Lake, Coconino Co., Arizona	42	22	17	77.3	8	4
Total		169	71	45			
Mean					63.4	7.0	3.2

[a]Vigor rating is an ocular estimate of the accession's general condition 1 = all dead; 5 = average vigor with some dieback; 10 = exceptional vigor with little or no dieback.

[b]Reproduction rating is an ocular estimate of the accessions reproduction: 1 = none; 5 = seedlings common but even aged; 10 = seedlings abundant and of several age classes.

(1953), and Beetle (1960) all recognized the distinctness of the North American forms, although each treated them in a different manner. We believe there are several com- pelling reasons for separation, which we will discuss.

Members of Seriphidium are Eurasian (and North African). Their center of distri- bution is Central Asia (Fig. 2). The present distribution suggests an evolutionary radi- ation from the areas of greatest species di- versity. On the basis of karyotypic, anato- mical, and morphological evidence, Filatova (1974) supported the view that the most primitive members of the Seriphidium occur in arid areas in Kazakhstan, USSR and adja- cent areas in Central Asia. She suggested an annual/biennial herbaceous species (*A. leuc- odes*) and a perennial shrub (*A. junceus*) as being ancient primitive types. Musaev (1965) gave detailed distribution maps of five species of Seriphidium, which indicate that the northern limit for these species is about 52°-53° N. latitude. Musaev con- tended that the Turan flora, composed in part of these Seriphidium members, is southern and Mediterranean and not strong- ly connected to the northern (grass-forb) steppes. This body of evidence suggests that Eurasian Seriphidium originated in Central Asia and radiated outward. Few members of the Seriphidium are found in northerly lati- tudes. The most widespread northern Old World species, *A. martima* (*sensu lato*) (Polyakov 1961, Clapham 1962), may have been able to migrate north in milder coastal habitats. The North American Tridentatae and at least two other *Artemisia* species re- main problematical—*A. palmeri* and *A. men- dozana*. *Artemisia palmeri* is largely her- baceous, is endemic to coastal badlands on both sides of the California-Baja California border, and little resembles the Tridentatae. Rydberg (1916) created a new genus for it— *Artemisiastrum. Artemisia mendozana*, pre- sumably from west central Argentina, is little known, but *Artemisia*, in general, is not prominent in South America (Bonpland et al. 1820, Harvard Univ. 1968, Heusser 1971, Good 1974). It was listed as a mem- ber of the Seriphidium by de Candolle (1837); Kawatani and Ohno (1964) indicated

that it was an octoploid (2n = 72).

Then, the fact that the Seriphidium and Tridentatae are advanced taxa, occurring in widely disjunct areas with no discovered pollen record in *Artemisia* profiles of the Beringia (Northeast Siberia-Alaska) area, further supports their taxonomic separation. *Artemisia* is a phylogenetically advanced genus in an advanced family (Compositae) (Stebbins 1974). Present consensus (Carlquist 1966, Cronquist 1968, Stebbins 1974) sup- ports a woody ancestral prototype for the Compositae. However, woodiness in *Arte- misia* is probably secondary. Most woody *Artemisia* species are bunched in Seriphi- dium and Tridentatae, which are specialized (reduced) in floral characteristics (Hall and Clements 1923). Anatomical characteristics of Tridentatae stems suggest an herbaceous ancestry (Diettert 1938, Moss 1940, Stebbins 1974). The Seriphidium do not presently oc- cur in northeastern Siberia nor the Triden- tatae occur in Alaska or adjacent areas of Canada (Fig. 1, 2). On the other hand, members of both the subgenera, Dracun- culus and particularly Artemisia (*sensu lato*), grow in those areas and span, or nearly span, Beringia (Rydberg 1916, Mizushima 1972, Korobkov 1972, Yurtsev 1972). No palynological evidence has been found to indicate that Seriphidium or Tridentatae were ever in Beringia (Hopkins 1967, Graham 1972). Most pollen identification of Ber- ingian *Artemisia* is only to the genus level; those samples that are identified to species are from the subgenus Artemisia. Furthermore, paleobotanists infer from pres- ent distributions and climates that *Artemisia* pollen from Quaternary deposits came from herbaceous species of the subgenus Arte- misia (Colinvaux 1967, Johnson and Packer 1967, Kind 1967). Although *Artemisia* is fairly common in Beringia, it is apparently not as prevalent as it was earlier during Quaternary time and reflects a harsher pres- ent day climate (Colinvaux 1967). Woody Chenopodiaceae of the same genera, but different species, often grow in association with the Tridentatae in North America and the Seriphidium in Central Asia (Musaev 1965, Blauer et al. 1976). Stebbins (1974)

believes that both chenopod shrubs and *Artemisia* shrubs of the Tridentatae and Seriphidium evolved from herbaceous ancestors on xeric "islands" of the Arcto-Tertiary Forest. In the case of *Artemisia*, the principally herbaceous, florally primitive subgenus Artemisia probably served as parental stock.

The limited data so far available indicate that the basic karyotypes of Tridentatae and Seriphidium are significantly different. Filatova (1974) presented idiograms of two species of Seriphidium which she considered to be primitive (Fig. 3), but Polyakov (1961) listed these taxa as being advanced. Currently, those two idiograms are the only ones available for diploid Seriphidium. We are preparing and will publish karyotypes of several Tridentatae taxa (McArthur, Pope, and Plummer, in preparation). Information presented here is tentative, coming as it does from small samples. Although there is variation throughout the section (Table 1), it appears that one basic genome is present which (with small changes) accounts for the chromosomal variation in the Tridentatae. Further evidence for one basic genome in the Tridentatae is the high in- cidence of multivalent formations in poly- ploid populations (McArthur and Pope 1975, McArthur, Pope, and Plummer, in preparation). Generally, diploid Tridentatae have a pair of large submetacentric chromosomes which may have a secondary con- striction in the long arm (Fig. 3), a pair of large metacentric chromosomes, three pair of medium metacentric chromosomes, two pair of medium submetacentric chromosomes, a pair of small metacentric chromosomes, and a pair of small subterminal chromosomes. In some cases (Table 1) a pair of medium subterminal chromosomes replaces the small metacentric chromosomes. The karyotype of tetraploid Tridentatae would appear to be an approximate doubling of the diploid karyotype (Table 2).

Karyotype evolution in several Compositae taxa often leads to: (1) shortening of absolute chromosome length, (2) less ho- mogeneity in chromosome lengths within the complement, and (3) rearrangements of chromosomal materials resulting in terminal centromere positions (Stebbins 1953, Huzi-

wara 1962, DeJong 1965, Anderson 1966, 1970). Based on these criteria, both the Se- riphidium and Tridentatae have advanced karyotypes as their morphologies suggest. Unpublished data (McArthur, Shrub Sci- ences Laboratory) indicate some American members of the subgenera Dracunculus and Artemisia have simpler karyotypes.

Chemotaxonomic studies have shown that section Tridentatae is a more or less natural group (Hanks et al. 1973, Kelsey et al. 1973, Geissman and Irwin 1974). Seriphi- dium members are probably less homo- geneous owing to their greater numbers and wider distribution. However, a particular sesquiterpene lactone, the anthelminic san- tonin, occurs widely in the old world Seri- phidium (Polyakov 1961), but santonin has not been discovered in any of the Triden- tatae (Geissman and Irwin 1974).

The Tridentatae are all woody shrubs, whereas about 15 percent of the Seriphi- dium are herbaceous and others are semi- shrubs with woody bases and herbaceous tops (Hall and Clements 1923, Polyakov 1961).

ORIGIN OF THE TRIDENTATAE

Artemisia is much more richly developed in Eurasia than it is in the Western Hemi- sphere. Consensus places the origin of the genus in Eurasia (Hall and Clements 1923, Beetle 1960, Stebbins 1974). Some workers, for example, Beetle (1960), believe that the section Tridentatae migrated to North America in a differentiated form. We be- lieve, however, that the North American Tridentatae differentiated in situ from her- baceous ancestors in the subgenus Artemisia. This subgenus is circumpolar at present, and evidence indicates that it was formerly even more prevalent in the northern latitudes (Colinvaux 1967, Estes 1968). Hall and Cle- ments (1923) pointed out that *A. bigelovii* shared traits found both in Abrotanum (Ar- temisia) and Seriphidium (Tridentatae). They thought *A. bigelovii* or *A. bigelovii*- like stock gave rise to the Tridentatae in the Southwest during the Pleistocene. They believed that with subsequent warming and drying, Tridentatae ancestors migrated north and developed into present-day taxa.

A study on the distribution of chromatographic patterns of phenolic constituents by Hanks et al. (1973) supports this view.

In either case, the Tridentatae have only been a prominent part of western American flora since the late Tertiary or early Quaternary periods (Axelrod 1950). The first *Artemisia* pollen recorded in the Intermountain Region is from Miocene Epoch deposits (Tidwell et al. 1972). Tridentatae progenitors probably were present on xeric "islands" in or near the North American Tertiary floras (Axelrod 1950). Alternating moist and dry climates during the Pleistocene Epoch favored the repeated evolutionary cycles that provided our present-day Tridentatae. Aridity is a powerful evolutionary stimulus (Axelrod 1972, Stebbins 1974).

It is interesting that arid, interior continental climates may have produced independently in western North America and Central Asia analogous series of woody *Artemisia*—the Seriphidium and the Tridentatae. An apparent similar example of convergent evolution is found in woody chenopod shrubs in the same two areas and in Australia.

Management Implications in Section Tridentatae

Although Tridentatae are recognized as a natural group, gross differences among section members have long been recognized. Black sagebrush (*A. nova*) has been regarded as a desirable, palatable species, but big sagebrush (*A. tridentata*) has been considered to be an unwanted range weed (Cottam 1961). We now know there is much variation within these taxa and that palatable and unpalatable forms occur in both (Stevens and McArthur 1974). In addition to the gross differences mentioned, there are many differences of smaller orders of magnitude. These last have led to differences of opinion among taxonomists.

Excluding *A. palmeri*, Rydberg (1916) recognized 13 species of Tridentatae, Hall and Clements (1923) 4 species, Ward (1953) 7, and Beetle (1960) 11. Each monographer (except Rydberg) also recognized subspecific taxa. Beetle (1960) and Beetle and Young (1965) divided the Tridentatae into 11 species, 9 subspecies, and 2 forms. Winward (1970) has suggested an additional form. Although we have learned much about sagebrush in the past 60 years, we have much to learn. Its ubiquitous western presence, its value as a soil stabilizer, its habitat and landscape value, and its attraction to the public will demand attention for a long time.

Range managers will benefit by learning as much as they can about variation in sagebrush. Characteristics of the subspecies of big sagebrush listed in Table 4 illustrate some differences in a group of closely related plants. It is difficult to separate these taxa by any one character, but taken in combination, each taxon is clearly distinct.

Such differences as adaptation, palatability, and height in these as well as in other sagebrush taxa should be taken into account in management decisions. This is not to say a manager should not make decisions on the basis of readily available information. We think that he should, but he should also realize that the knowledge base is expanding.

Some broad aspects of shrub management were discussed in the introduction. We pointed out that some taxa are widely adaptive. In looking at shrub adaptation in a narrower sense, it can be important for us to consider sources of particular taxa individually. On specific sites, different accessions of the same plant taxon may perform differently as do the subspecies of big sagebrush (*A. tridentata*) in a uniform garden (Table 3). Marchand et al. (1966) also observed differential performance of big sagebrush taxa in a uniform garden. As one might expect, the same accessions may perform differently on different sites. Some seem to have broader amplitudes of adaptation than others. In a paired performance (establishment, production, and reproduction) several accessions of Tridentatae in the taxa, *A. tridentata tridentata, A. nova, A. cana*, and *A. bigelovii,* showed differential adaptation. Nine accessions performed equally well at two sites in central Utah (Snow Field Station near Ephraim and Gordon Creek Winter Game Range near Helper), but seven performed markedly better at one or the other of the sites. When considering seed sources for a seeding, it is best to

TABLE 4. Characteristics of subspecies of *Artemisia tridentata*.

| Characteristic | Subspecies | | | References |
	tridentata	*vaseyana*	*wyomingensis*	
Habitat and range	Foothills and valley floors. 610-2140 m. British Columbia and Montana to Baja California and New Mexico.	Foothills and mountains. 915-3030 m. British Columbia and Alberta to California and New Mexico.	Foothills and valley floors. 1520-2150 m. Montana to Arizona.	This paper; Beetle and Young 1965; McArthur et al. 1974.
Smell	Bitter pungent	Pleasant	Bitter pungent	McArthur et al. 1974.
Leaf shape	Narrowly cuneate to oblanceolate	Cuneate	Cuneate	Marchand et al. 1966; McArthur et al. 1974; McDonough et al. 1975.
Height	1.0-4.0 m	0.7-1.2 m	0.5-0.8 m	McArthur et al. 1974.
Sesquiterpene lactone compounds	4-7	3-6	2	Kelsey et al. 1973.
Ultraviolet visible coumarins	Trace	Abundant	Trace	Shafizadeh and Melinkoff 1970; Stevens and McArthur 1974; Brown et al. 1975.
Tendency to layer	None	Strong	None	Beetle and Young 1965.
Palatability to deer and sheep	Low	High	Intermediate	Hanks et al. 1973; Sheehy and Winward 1976.
Protein content	High	Low	Low	Sheehy and Winward 1976; Welch et al. 1977.
Seed germination	High	Low	Intermediate	Harniss and McDonough 1976.
2n	18,36	18,36	36	Ward 1953; Taylor et al. 1964; Winward 1970; Kelsey et al. 1975; McArthur, Pope, and Plummer (in prep.)
Flower and seed phenology	Late	Early	Late-Intermediate	Marchand et al. 1966; Winward 1970; Hanks et al. 1973.

obtain seed from a site as similar and as close as possible to the site to be seeded. If seed must be brought in from some dis tance, it is best to get it from a harsher cli mate or more northerly location (Plummer et al. 1968, Plummer 1977). For ex ample, accessions of *A. bigelovii* from nearby Emery County, Utah, perform much better at the Snow Field Station and the Gordon Creek Winter Range than those from the more distant and southern San Juan County, Utah, and Coconino County, Arizona. Van Epps (1975) presented data supporting a similar conclusion for fourwing saltbush (*Atriplex canescens*). Although the foregoing discussion is based on wilding transplant experiments, we have noted dif ferential success of accessions of big sage brush on seeded areas.

The sagebrushes are a valuable resource, which can be more valuable if managed wisely. Wise management entails maintain ing productive natural populations, seeding to improve depleted or disturbed ranges, and thinning closed stands. When mixed with grasses, forbs, and other shrubs sagebrush adds beauty to the range, food and cover for animals, and stability to the soil. More over, sagebrush variation should permit se lection of material for particular purposes, such as palatable, high-protein forms for mule deer winter ranges. We think that such an opportunity exists, since putative natural hybrids have been discovered (Ward 1953, Beetle 1960), and we have cytological and artificial pollination data that hybridi zation occurs (McArthur and Pope 1975, McArthur, Pope, and Plummer, in prepara tion). We predict that in the years ahead the much-maligned sagebrush will be re garded with increasing favor by land man agers.

Acknowledgments

Note Added in Proof

Since this paper went to press, we learned of a monographic study on the cytotaxonomy of the *Artemisia maritimia* complex of section Seriphidium (Persson, K. 1974. Biosystematic studies in the *Artemisia maritima* complex in Europe. Opera Bot anica 35:1-188). Persson's karyotypes of diploid *A. santonicum* are apparently more primitive than those shown by Filatova (1974). However, the *A. santonicum* karyo types are unlike the Tridentatae karyotype.

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